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Spatial and temporal variation of roots, arbuscular mycorrhizal fungi, and plant and soil nutrients in a mature Pinot Noir (*Vitis vinifera* L.) vineyard in Oregon, USA

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Abstract

The spatial and temporal development of grapevine roots and associated mycorrhizal fungi was studied in 1999 and 2000 in a 21-year-old, Pinot Noir (*Vitis vinifera* L.) vineyard located on a Jory soil (Palehumult, silty clay loam) in Oregon, USA. The density of woody roots and fine (primary) roots deemed to be physiologically active (based on color and cellular integrity) were determined at monthly intervals in the weed-free, vine row and in the alleyway between rows at two depths (0–50 and 50–100 cm). The majority of fine roots were growing in the vine row at 0–50 cm depth. Fine root density did not change dramatically over the 1999 or 2000 seasons until the time of fruit harvest in the fall. Apparently, new root growth kept pace with turnover (death) prior to harvest, but new root growth surpassed turnover in the fall after fruit harvest. Colonization of fine roots by arbuscular mycorrhizal fungi (AMF) was consistently high in the vine row at 0–50 cm depth, but was lower in roots growing in the alleyway, and in roots below 50 cm. The proportion of fine roots containing arbuscules (the site of nutrient exchange in arbuscular mycorrhizas) was also greatest for roots growing in the vine row at 0–50 cm depth. Arbuscular colonization of these roots increased prior to budbreak in the spring, reached a high level (50–60% root length) by early summer, and remained high until after the time of leaf senescence in late fall. Arbuscular colonization decreased rapidly by December of 1999 when November rainfall exceeded 200 mm, but did not decline by December of 2000 when November rainfall was below 80 mm. The availability of important plant nutrients in the soil, with the exception of Mg and Zn, was higher in the upper 50 cm of the soil profile where the majority of roots were found. In addition, available nitrate and phosphate were higher in the vine row than in the alleyway soil. Seasonal changes in leaf nutrient concentrations of Pinot Noir confirmed findings in other cultivars, but fluctuations of N, P, and K concentrations in fine roots over the season suggested that fine roots may play a role in nutrient storage, as well as nutrient uptake, in grapevines. Grapevines grown in Oregon direct significant resources to roots and AMF after fruit harvest and substantial post-harvest nutrient uptake may extend into the early winter.

Introduction

The roots of grapevines (*Vitis* spp.) are often heavily colonized by arbuscular mycorrhizal fungi (AMF) under field conditions (Possingham and Obbink, 1971; Schreiner, 2003; Schubert and Cravero, 1985). In some cases, AMF appear to be necessary for normal growth and survival of field-planted grapevines (Menge et al., 1983). Studies conducted in sterilized soils in pots have shown that AMF enhance the uptake of P, Zn, and Cu in grapevines (Biricolti et al., 1997;

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Karagiannidis et al., 1995; Petgen et al., 1998), and that colonization of roots by AMF can increase the drought tolerance of grapevines (Nikolaou et al., 2003). Little is known, however, about the seasonal and spatial development of mycorrhizal fungi in vineyard soils. In addition, knowledge of the spatial and temporal dynamics of grape root development remains unclear.

While it is generally thought that the majority of grape roots occur within the upper 50–60 cm of the soil profile (Richards, 1983), roots that penetrate soils below this depth are not uncommon (Mohr, 1996; Southey and Archer, 1988) and certainly play a role in water uptake. The generally accepted model for the growth dynamics of grapevine roots is that root growth begins about 4–6 weeks after shoot growth has commenced, reaching a maximum near the time of flowering, declining thereafter and sometimes showing another smaller increase at the time of (or shortly after) fruit harvest (Freeman and Smart, 1976; Mullins et al., 1992; Van Zyl, 1988). However, some studies have reported root growth to occur prior to shoot growth in the spring (Loubser and Meyer, 1986; Reimers et al., 1994). Recent work conducted on 16-year-old vines in Germany showed that root growth increased slowly until the time of flowering when the rate of growth increased substantially and remained at a high rate until harvest (Mohr, 1996). Mohr (1996) suggested that the different root growth patterns observed in vineyards were the result of warm vs. cool climatic conditions. It is well known that the type and quantity of irrigation water applied to vineyards can exert a strong influence on the extent and timing of root growth (Freeman and Smart, 1976; Van Zyl, 1988). It is unclear from these studies when periods of root growth would be expected to occur in Oregon vineyards owing to the cool climate, wet winters and dry summers, and the low fertility of most of Oregon's viticultural soils.

Past studies on roots in vineyards agree that the root density of grapevines is very low in comparison to other crops (for discussion see Mohr, 1996). Since AMF play a more significant role in plants with low root densities or with relatively coarse fine roots like grapevines produce (Abbot and Robson, 1984; Baylis, 1975; Hetrick, 1991; Koide 1991), understanding how both roots and AMF developed in soil throughout the year is important. Knowledge of the spatial distribution and seasonal dynamics of roots and AMF together will provide viticulturalist's with more complete information to manage the below-ground ecosystem in vineyards.

The objectives of this research were to determine when and where grapevine roots and mycorrhizal fungi were actively growing in a typical Oregon vineyard soil and to better understand how soil water and nutrient availability may influence root and AMF development. In addition, the seasonal changes of leaf and fine root nutrient concentrations were examined to better understand how plant nutrient status relates to below-ground activities of roots and AMF.

Materials and methods

Site description and sampling strategy

The study took place in a 21-year-old, self-rooted, dryland Pinot Noir (*Vitis vinifera* L., clone FPMS 4) vineyard at the Oregon State University Research Vineyard located in Alpine, OR, USA (44°20′ N, 123°24′ W). This site was chosen because the soil (Jory series, Palehumult, silty clay loam) is representative of many Oregon vineyards, and because this field was managed as a commercial vineyard. The vineyard is located on a south-facing slope, 200 m above sea level, and receives ~1100 mm rainfall per annum primarily during the fall, winter, and spring. Vine rows were oriented on a north–south axis. The vineyard was planted in 1978 at a density of 2000 vines ha^{-1} with 1.82 m between vines in the row and 2.74 m between rows. Vine rows were kept weed-free during the summer by applying glyphosate at the label rate (Roundup, Monsanto, St. Louis, MO, USA) in a 1 m wide strip in the spring of each year. Alleyways (~2 m) had resident vegetation comprised mainly of red fescue (*Festuca rubra* L.), ryegrass (*Lolium* spp.), annual bluegrass (*Poa annua* L.), and crimson clover (*Trifolium incarnatum* L.), but containing small amounts of common weeds including falsedandelion (*Pyrrhopappus* sp.), sorrel (*Rumex* sp.), geranium (*Geranium oreganum* Howell), and mustards (*Brassica* spp.). The alleyways in this vineyard were managed by tilling (power spader

to a depth of 30 cm) alternate alleys in the late spring and by mowing the vegetation in the opposing, untilled alleys in the spring and summer as needed.

Vines were head pruned in late January or early February and an average of 16 buds (~9 buds m^{-1} linear vine row) were retained on each vine both years. Fruiting canes were trained upright on a Gouyot trellis with the base wire 90 cm above the ground. Canes were hedged in mid to late July at a height of ~2.3 m from the ground. Fruit was thinned in both years shortly before veraison (onset of ripening and color change of berries) to an average of 20 clusters per vine. Leaves on the east side of the canopy in the fruiting zone were removed after the onset of veraison to allow approximately 50% solar exposure on fruit clusters during the morning hours.

The development of roots and AMF were monitored within the brown-colored, high-organic matter, topsoil (0–50 cm, A horizon) and the red-colored, low-organic matter, subsoil (50–100 cm, B horizon) at monthly intervals from April through December of 1999 and 2000. The division between the A and B horizon in this soil varied between 40 and 60 cm depth, and on some occasions the 50–100 cm samples contained soil and parent material (weathered basalt) from the C horizon. Root densities and AMF colonization were compared between the weed-free (1 m herbicide treated strip) vine row and the alleyway between rows. Alleyway samples were only collected from those alleys that were tilled in the prior year (mowed alleys in the current year) to avoid possible tillage effects on roots and mycorrhizae within the same year. Data were collected from four replicate sampling locations along a diagonal transect across the vineyard. Each replicate sampling location was comprised of 10 sample vines and was further divided into two root sampling zones (vine row vs. alleyway) and two root sampling depths. Data within a given year were collected from the same replicate locations, but different transects were used in 1999 and 2000.

Below-ground variables

Root and soil samples were obtained with a soil corer (3.1 cm diameter) capable of sampling to a depth of 1 m (JMC ESP+, Clements Associates Inc., Newton, IA, USA). Soil samples were collected at the beginning of each month (± 4 days) from April until December in both years and in February of 2000. Five soil cores were collected from the vine row zone (within the weed-free zone) and five cores were collected from the alleyway zone (within the resident vegetation between vine rows) at each replicate sampling location (10 cores at each sampling location for a total of 40 cores per sampling date). Soil core samples (in polyethylene liners) were placed in insulated boxes for storage and transport to the laboratory. Each sample consisting of five soil cores collected from the vine row or alleyway zone at each replicate sampling location was divided into two depth layers between 0–50 and 50–100 cm (2×2 factorial with four replicates giving a total of 16 samples per sampling date). Samples were gently mixed and stored at 4 °C in plastic bags for up to 2 weeks before processing.

Subsamples were removed to determine soil moisture (~75 g), soil chemical properties (~100 g), and AMF hyphal lengths (~20 g). Any grape roots present in the subsamples were removed and placed with the root samples collected below. Soil moisture was determined on all samples gravimetrically, weighing samples before and after oven drying at 110 °C for 7 days (Gardner, 1986). Soil nutrient availabilities and pH were determined after air-drying for 7 days at ambient temperature. Soil chemical analysis was conducted on samples representing both the vine row and alleyway sampling zones at both depths (0–50 and 50–100 cm) collected on May 4, 1999. In 2000, soil chemical analysis was carried out using the topsoil only (0–50 cm). Analysis was conducted on soil samples collected from the vine row on May 1, and August 3, 2000, and from the alleyway on August 3, 2000. The length of extraradical, AMF hyphae in soil was determined using the filtration-gridline method of Sylvia (1992), as modified by Bethlenfalvay et al. (1999) in duplicate. Extraradical hyphae are those hyphae that grow outside the root and function in nutrient uptake from soil (Smith and Read, 1997). Subsamples for hyphal analysis were immediately frozen and stored at −20 °C. Samples were later thawed, mixed, and a 10 g sample was used for the analysis. AMF hyphal lengths were determined for both vine row and alleyway sampling zones at both sampling depths

in June, August, and October of 1999. Hyphal lengths were expressed per unit of soil volume using a soil bulk density of 1.3 g mL^{-1}.

Grapevine roots were carefully handpicked from the remaining soil and combined with any roots retrieved from the subsamples above. Roots were isolated from small aliquots of the sample (~250 mL) at a time, until all of the soil was processed. This step was repeated. This approach was more efficient (time wise) than the more traditional washing and sieving approach often used to extract roots (Böhm, 1979) because the samples were relatively large, the clay content and soil aggregate stability was high, and the organic matter content (including numerous non-grape roots both living and dead) of the soil was very high. Roots obtained (including those non-grape roots that were similar in appearance to grape roots by the naked eye) were washed over a 500 μm sieve, and separated into two fractions in water. Grape roots were then separated from the roots of other plants based on their size, color, and morphology under a stereoscope. Roots from other plants in the vineyard were dug up and examined for comparison purposes. Efficiency of grape root extraction was assessed on a number of occasions by exhaustively washing and sieving samples that had been previously handpicked. More than 90% of the grape fine root fresh mass was obtained by the handpicking method and the vast majority of those roots still present in the soil were very small fragments (< 3 mm in length).

Woody grape roots of all diameters were included in a single fraction (class C, D, and E as defined by Mohr, 1996). Small diameter woody roots (1–3 mm) were distinguished from fine roots by the loss or collapse of the cortex. Only those woody roots containing a white colored periderm or stele were included. Fine roots were defined as primary roots with an intact cortex varying in color from white to brown (class A and B as defined by Mohr, 1996). Root fractions were blotted dry and weighed. The length of woody roots was measured with a ruler. Fine roots were stored in FAA (formaldehyde/acetic acid/alcohol 5%:10%:50% v/v) for up to 2 months before clearing and staining to assess AMF colonization. Roots were cleared and stained using KOH, H_2O_2, and trypan blue as in Schreiner (2003).

Fine root length was determined by the gridline intercept method (Newman, 1966) under a stereoscope. Colonization of fine roots by AMF was determined on randomly selected root fragments using the method of McGonigle et al. (1990), as modified by Schreiner (2003). Total AMF colonization included vesicles, arbuscules, coils, and nonseptate hyphae within the root cortex. Arbuscular colonization was assessed separately. Arbuscules are specialized, ephemeral structures produced within root cortical cells that are believed to be the site of nutrient exchange between plant and fungus in arbuscular mycorrhizas (Blee and Anderson, 1998; Smith and Read, 1997). A minimum of 100 root intersections was examined for a given sample. The lengths of both woody and fine roots were expressed per unit volume of soil based on the volume of the sampling cores.

In 2000, separate samples of fine roots were collected from June through November to determine mineral nutrient concentrations. Fine roots collected for mineral tests were obtained from 2 to 4 vines located in a vine row opposite the data vines from 0 to 50 cm depth by hand digging. Sampling positions were marked to avoid future sampling in the same region. Roots used for this analysis were handpicked from the soil using the same criteria as above. Roots were sonicated for 30 s in a water bath sonicator (Ultrasonic LC 60, Lab-Line Instruments Inc., Melrose Park, IL, USA) and rinsed in distilled water to remove adhering soil particles prior to oven drying. Four fine root samples were collected at each sample date.

Above-ground variables

The day that budbreak, 50% bloom, 50% veraison (berry color change), harvest, and leaf-fall occurred was noted. Cane lengths were measured at the beginning of May, June, and July in both years by measuring a single, representative cane (agreed upon by two observers from across the alleyway) on each of the ten data vines. Two leaf samples for nutrient determinations were collected at each replicate sampling site. A mature leaf opposite the flower or developing fruit cluster and a most recently, fully expanded leaf from the same shoot were collected from each vine. Leaves from vines 1 through 5, and from vines 6

through 10 were pooled, and analyzed separately. Leaves (without petioles) were collected from June through November in each year, washed in distilled water, oven-dried, ground to pass a 40 mesh, and analyzed for mineral nutrient concentrations. Fruit yield (cluster fresh mass) was determined on each of the 10 vines per replicate sampling site. A random sample of five clusters from each replicate was crushed and pressed to measure soluble solids. Percentage of juice soluble solids (°Brix) was determined with a refractometer (Leica Microsystems, Buffalo, NY, USA).

Soil and plant tissue nutrient analysis

Analysis of soil and plant tissue nutrients was conducted by the Oregon State University Central Analytical Laboratory using standard procedures for Western Oregon. Soil pH and B were determined in water extracts; NO_3 and NH_4 after KCl extraction; P by Bray-1 method; K, Ca, and Mg after ammonium acetate extraction; and Fe, Zn, Mn, and Cu after DTPA extraction. Leaf and fine root nutrient concentrations were determined after dry-ashing (except for N). N was determined via combustion analysis (CNS-2000 Macro Analyzer, Leco Inc., St. Joseph, MI, USA). P, K, Ca, Mg, Fe, Mn, Cu, B, and Zn were measured by ICP-OES (Perkin Elmer Optima 3000DV, Wellesley, MA, USA).

Data analysis

All data were analyzed by multifactor ANOVA using a significance level of 95% confidence ($p < 0.05$). Soil moisture, root length, and AMF colonization variables were log transformed to overcome violations of homogeneity of the variance. Main effects and interactions between year, sample date (month), soil sampling zone (vine row vs. alleyway), and depth were analyzed. Because many of the subsoil samples (0–50 cm) did not have enough roots to accurately quantify AMF colonization, multiple ANOVAs excluding one of the four main factors were conducted to analyze effects on AMF colonization. Higher order interactions were removed from the models when not significant. Soil nutrient availabilities and pH were analyzed using nonparametric techniques and means were compared using Mann–Whitney test at 95% confidence. Leaf nutrient concentrations were analyzed by ANOVA using year and sample date as factors. Fine root nutrients (determined in 2000 only) were analyzed by single factor ANOVA. Mean values and the standard error of the mean are presented for all data.

Results

Climate, vine growth and phenology, and soil moisture

There were significant differences in weather patterns between 1999 and 2000. Rainfall prior to budbreak was greater in 1999 than 2000, while more rain fell in May and June of 2000 (35 mm) than the same period in 1999 (Figure 1). Rainfall from July through October was very similar in both years, but rainfall was much greater in 1999 after harvest. Temperatures were different between the two years of this study. Average air temperatures showed a much warmer spring and early summer in 2000, as compared to 1999 (Figure 1). Warmer temperatures in 2000 resulted in an accumulation of ~110 more Growing Degree Days (°C base 10) by July 1, as compared to 1999. Vines developed at a faster rate in 2000 as a result of the higher temperatures. Budbreak, bloom and veraison occurred 7–10 days earlier in 2000, as compared to 1999 (Table 1). Harvest was 2 weeks earlier in 2000. Early season cane growth was significantly greater in 2000 ($p < 0.05$), the average cane length by July 6 was 30% greater in 2000 than in 1999 (data not shown). The pruning mass of vines collected during the dormant period in 1999 was lower than in 2000 by about 12%, but this was not statistically significant (Table 1). The fruit yield from this Pinot Noir vineyard averaged 2.73 and 2.78 kg vine^{-1} in 1999 and 2000, respectively. This is equivalent to ~5.5 t ha^{-1}.

Changes in soil moisture in the vine row and alleyway at two depths over two years are shown in Figure 2. Soil moisture levels in the topsoil and subsoil showed similar trends between years, although soil moisture was higher in the topsoil in the spring of 1999 as compared to 2000, which corresponded with higher rainfall prior to budbreak in 1999. Another difference between years

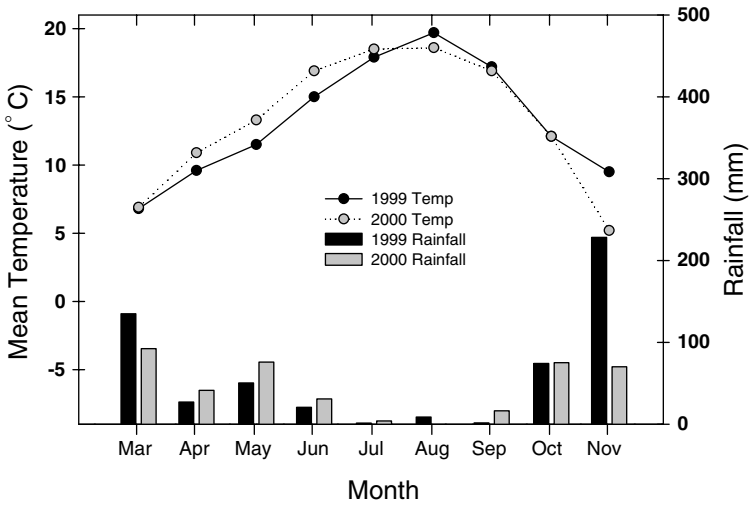

Figure 1. Mean monthly air temperatures and cumulative monthly rainfall recorded at Corvallis, OR, USA between March and November in 1999 and 2000.

Table 1. Phenology, yield, and vigor of 21-year-old Pinot Noir grapevines studied in 1999 and 2000

Growth stage	1999	2000
Date reached		
Budbreak	April 30	April 23
Bloom (50% capfall)	July 1	June 22
Veraison (50% berries colored)	September 8	August 28
Harvest	October 19	October 5
Leaf-fall	November 5	November 10
Yield and vigor		
Fruit yield (kg vine^{-1})	2.73	2.78
Soluble solids (°Brix)	24.0	24.2
Pruning mass (kg vine^{-1})	0.64	0.72

was that soil moisture in the alleyway declined more rapidly than in the vine row in the late spring of 1999 only (Figure 2). This difference was probably due to a combination of both earlier mowing of the alleyway vegetation in 2000 and slower canopy development of Pinot Noir in 1999. Soil moisture was replenished more rapidly in the fall of 1999 than in 2000, due to an earlier onset of fall rains in 1999 (Figure 1). In both years, soil moisture in the vine row and alleyway topsoil (0–50 cm) reached a low value of 115–120 g kg^{-1} soil in September and October, which corresponds to a soil water potential of approximately −1.0 MPa for this soil (Schreiner, unpublished).

Soil nutrient availabilities

Analysis of available soil nutrients in May 1999 showed that both macro- and micro-nutrients, except Mg and Zn, occurred at much higher concentrations within the topsoil (0–50 cm) than the subsoil (50–100 cm, Table 2). Soil pH was higher also in the topsoil than the subsoil. Differences in soil pH between years (May 1999 vs. May 2000 for vine row topsoil) were not significant. Soil nitrate availability was higher in the vine row than in the alleyway topsoil in May 1999 and in August 2000 (Table 2). Soil P was higher in the vine row than the alleyway in August 2000, but not in May 1999. Soil B was higher in the vine row than the alleyway in May 1999, but not in August 2000. Soil P, Fe, Mn, Cu, and Zn were at higher concentrations in August than in May of 2000.

Root distribution and development

The density of woody grape roots measured in this vineyard was most often below 0.2 mm mL^{-1} soil (Figure 3a). Variation within the woody root length data was quite high throughout the experiment and seasonal trends were not apparent. However, woody roots were more prevalent in the vine row than the alleyway and more prevalent in the topsoil than the subsoil over the course of the entire study. The main

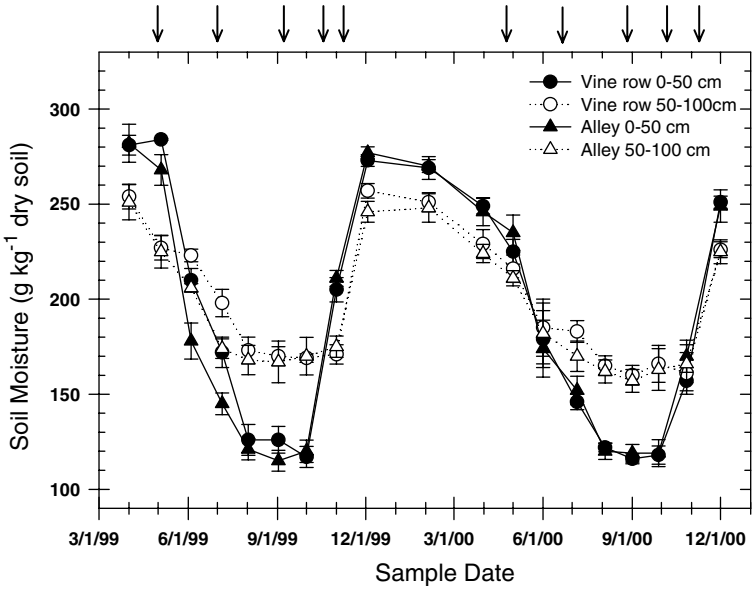

Figure 2. Soil moisture concentrations within the vine row and alleyway at two depths in the soil profile in 1999 and 2000. Each symbol represents the mean value with standard error ($n = 4$). Five arrows above the figure in each year indicate the time of bud-break, bloom, veraison, harvest, and leaf-fall.

Table 2. Soil nutrient availabilities (mg kg^{-1} dry soil) and pH in Jory soil sampled at various times, locations, and depths during 1999 and 2000 ($n = 4$)

Nutrient	May 1, 1999				May 4, 2000	Aug 1, 2000	
	Vine row		Alley		Vine row	Vine row	Alley
	0–50 cm	50–100 cm	0–50 cm	50–100 cm	0–50 cm	0–50 cm	0–50 cm
NH_4 (se)	12.3 b (1.5)	2.2 a (0.2)	9.1 b (0.8)	2.2 a (0.2)	2.5 a (0.4)	4.1 a (1.1)	1.9 a (0.2)
NO_3 (se)	4.0 b (0.9)	0.6 a (0.2)	0.7 a (0.2)	0.5 a (0.1)	4.5 b (0.6)	5.1 b (1.8)	0.5 a (0.0)
P (se)	12.0 b (1.9)	3.8 a (0.3)	9.5 b (0.9)	4.0 a (0.0)	13.7 b (1.8)	30.7 c(4.2)	15.3 b (2.8)
K (se)	198 b (20)	91 a (2)	204 b (5)	104 a (4)	175 b (10)	174 b (23)	168 b (11)
Ca (se)	646 b (106)	306 a (10)	651 b (37)	301 a (29)	451 ab (66)	491 ab (81)	416 ab (111)
Mg (se)	73(19)	73(18)	52(3)	79(22)	76(8)	70(23)	76(20)
Fe (se)	21.7 c(1.3)	8.7 a (0.7)	20.0 bc(1.1)	8.0 a (0.7)	15.3 b (1.3)	33.1 d(3.5)	37.7 d(7.6)
Mn (se)	13.4 d (1.9)	2.5 ab (0.5)	13.6 d (1.5)	2.1 a (0.4)	4.7 bc (0.5)	12.3 d (1.7)	9.5 cd (2.0)
B (se)	0.82 b (0.11)	0.30 a (0.04)	0.35 a (0.03)	0.25 a (0.03)	0.63 b (0.06)	0.85 b (0.08)	0.50 ab (0.10)
Cu (se)	0.75 bc (0.19)	0.06 a (0.01)	0.39 b (0.05)	0.07 a (0.01)	0.65 b (0.07)	2.69 d (0.35)	1.82 cd (0.77)
Zn (se)	0.77 ab (0.20)	0.34 ab (0.22)	0.27 a (0.04)	0.56 ab (0.25)	0.41 a (0.04)	1.37 b (0.26)	1.02 ab (0.56)
pH (se)	5.38 b (0.14)	5.10 a (0.0)	5.42 b (0.03)	5.10 a (0.0)	5.57 b (0.08)	5.55 b (0.09)	5.65 b (0.11)

Means followed by the same letter across rows are not significantly different (Mann–Whitney nonparametric test at 95% confidence).

effects of sampling zone (vine row vs. alley) and depth on woody root length were significant by ANOVA ($p < 0.05$). The density of fine roots in the topsoil (0–50 cm) ranged from 0.1 to 1.2 mm mL^{-1} soil, while those in the subsoil ranged from 0 to 0.15 mm mL^{-1} soil (Figure 3b). Fine roots clearly developed to a much greater extent in the topsoil than the subsoil (Figure 3b), which was less apparent for the woody roots (Figure 3a). Fine roots were more numerous in

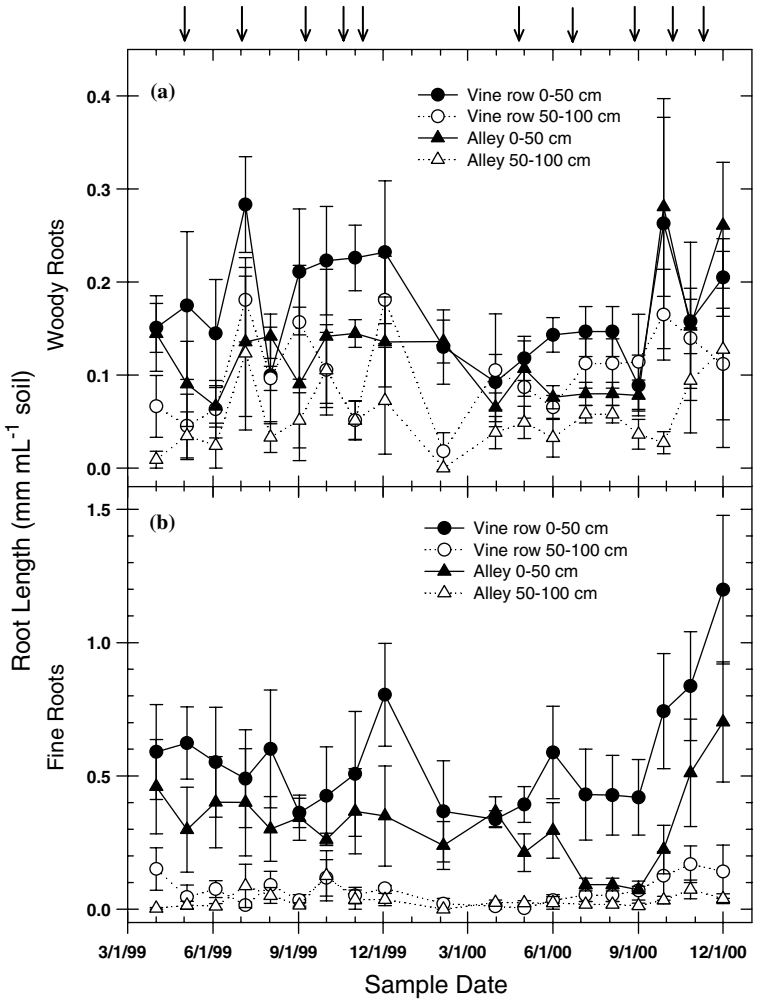

Figure 3. Woody (a) and fine (b) root length of Pinot Noir grapevines within the vine row and alleyway at two depths in the soil profile in 1999 and 2000. Symbols and arrows as in Figure 2.

the vine row than the alleyway, similar to woody roots. The main effects of sampling zone (vine row vs. alley) and depth on fine root length were also significant by ANOVA ($p < 0.05$). When comparing both years, a small but consistent seasonal trend was found, such that fine root length increased in the fall of both years reaching the maximum values observed in both years in early December (Figure 3b). This increase was more pronounced in 2000 than in 1999.

A robust measure of where most roots were growing in this vineyard was obtained by averaging the data from all 19 sampling dates. This analysis showed that 59% of the fine root length occurred in the vine row and 31% occurred in the alleyway at a depth of 0–50 cm. Only 10% of the fine root length was found below 50 cm in both the vine row and alleyway combined. Lower values of 39% and 27% of grape woody root length were found in the topsoil (0–50 cm) of the vine row and alleyway, respectively. Thirty-four percent of woody root length was found below 50 cm. So, nearly a third of the woody roots were extracted from the subsoil (50–100 cm), but they were only supporting 10% of the vines fine roots at that depth.

Mycorrhizal colonization of fine roots

AMF colonization of fine roots was consistently high for roots growing in the vine row in both years (Figure 4a). The presence of AMF

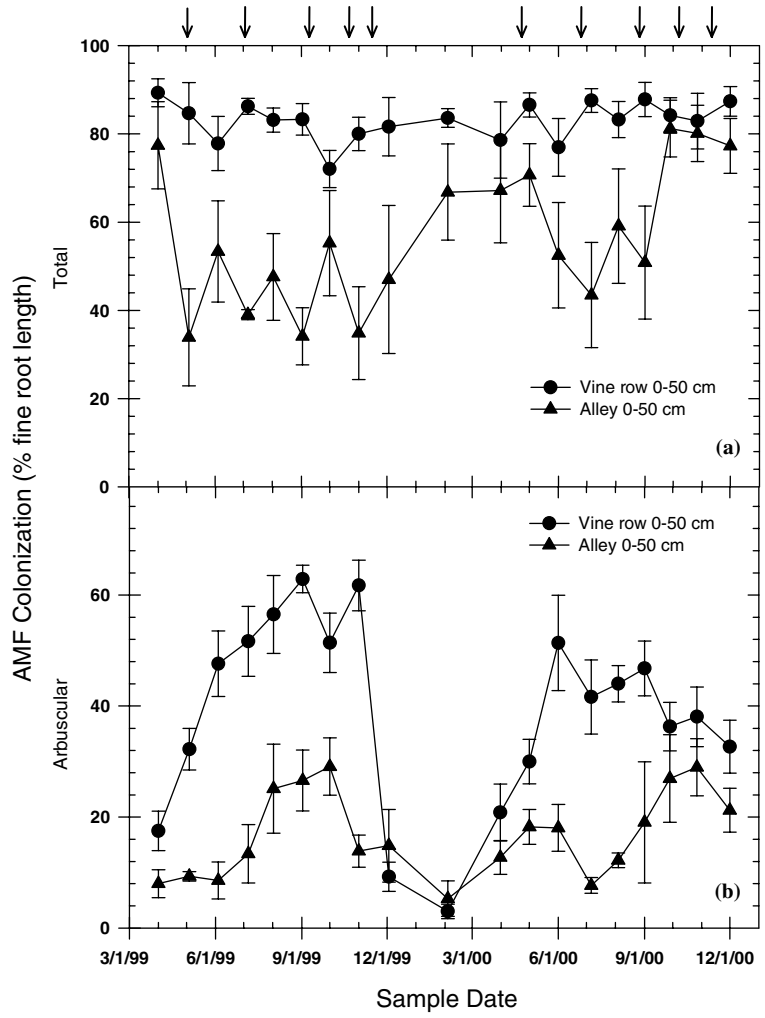

Figure 4. Total mycorrhizal (a) and arbuscular (b) colonization of fine roots of Pinot Noir grapevines within the vine row and alleyway at 0–50 cm depth in 1999 and 2000. Symbols and arrows as in Figure 2.

structures in fine roots from the vine row was always above 70% of root length and averaged 84% over all sample dates. The intensity of colonization by AMF in these roots isolated from the vine row was often exceptional. Multiple strands of hyphae were often found between each layer of cortical cells and arbuscules were often observed in every cortical cell in many fine roots. Fine roots growing in the alleyway (tilled the previous year) were not as heavily colonized by AMF as those in the vine row, except late in the 2000 season. Fine roots growing in the subsoil (50–100 cm) averaged 49% colonization for roots in the vine row and 32% colonization for roots in the alleyway over all dates (data not shown).

Arbuscular colonization, which presumably reflects an active exchange of nutrients between roots and mycorrhizal fungi, showed much greater seasonal variation than the total AMF colonization of roots. A clear seasonal trend was found for both years in those fine roots growing in the topsoil of the vine row (0–50 cm). Arbuscular colonization increased from about 20% at budbreak to about 50% by June or July (Figure 4b). Arbuscular colonization remained at high levels until after leaf fall in November (Figure 4b). Significant differences in arbuscular colonization were found between 1999 and 2000. Arbuscular colonization rose more quickly in 2000 (a warmer year), but did not reach as high a level in

mid summer as occurred in 1999. In addition, arbuscular colonization decreased to near zero between November and December of 1999 (very high rainfall and shorter post-harvest period), but remained at a high level to December of 2000. Arbuscular colonization was much greater for roots growing in the vine row than the alleyway topsoil. Arbuscules were found in roots collected from the subsoil (50–100 cm), but at much lower levels than roots from the topsoil. Roots growing in the subsoil of the vine row averaged 21% arbuscular colonization, while roots in the subsoil of the alleyway averaged 6.2% arbuscules over all sampling dates (data not shown).

The length of extraradical hyphae of AMF did not change significantly over the 1999 growing season and these data were not collected in 2000. The average values of external AMF hyphae over three sampling dates in 1999 were 13.3 m mL^{-1} soil in the vine row at 0–50 cm depth, 1.3 m mL^{-1} soil in the vine row at 50–100 cm depth, 5.8 m mL^{-1} soil in the alleyway at 0–50 cm depth, and 1.0 m mL^{-1} soil in the alleyway at 50–100 cm depth (data not shown). Soil hyphal lengths obtained within each sampling zone by depth combination were highly correlated ($r > 0.90$) to fine root lengths of grape at all sampling dates examined. The length of AMF hyphae in soil was on average 19,000 times greater than the length of fine grape roots.

Leaf and root nutrient concentrations

Concentrations of leaf nutrients between June and November of both years were nearly identical and showed the same seasonal trends, so only the 2000 data are shown in Figure 5. Both macro- and micro-element concentrations in the leaves changed significantly ($p < 0.05$) over the growing season. Leaf N and P concentrations were highest at the beginning of the season and declined dramatically over the summer (Figure 5a). The opposite trend occurred for Ca and Mg, while K concentrations in leaves showed little change over the season. Only leaf N and P dropped significantly in concentration between October and November, showing that these nutrients were remobilized from senescing leaves prior to leaf-fall. Leaf micronutrients B and Zn did not change appreciably over the season, while leaf Cu decreased over the season and leaf Fe and Mn increased late in the season (Figure 5b). No micronutrients appeared to be remobilized out of leaves prior to leaf-fall. Seasonal changes in leaf nutrients that were found in these Pinot Noir vines were generally similar to previous findings for winegrapes (Boselli et al., 1998; Christensen, 1984; Colugnati et al., 1997; Conradie, 1981b; Hiroyasu, 1961).

Changes in the fine root mineral concentrations over the course of the 2000 season were striking (Figure 6). N, P, and K concentrations in roots were at high levels on June 1, declined precipitously by July 6 (N and P) or August 1 (K), and then began to increase in mid to late summer (Figure 6a). N, P and K concentrations in fine roots did not recover to the same high level by the end of the season as they were at the beginning of June. Mg concentrations in fine roots showed a declining trend over the growing season, but this was not significant by ANOVA ($p = 0.058$). Calcium concentrations in fine roots did not significantly change over the season. Micronutrient concentrations in fine roots showed relatively small changes over the course of the growing season. Fe and Zn concentrations in fine roots increased over the summer and into the fall, while B concentrations in fine roots increased after June and then declined during the fall. Fine root Mn concentrations went up and down without a clear seasonal trend. Cu went up slightly in the fall but this was not significant by ANOVA ($p = 0.054$).

The scale of Figures 5 and 6 are identical so that comparisons between leaf and fine root nutrient concentrations can be made. N concentrations were considerably higher in the leaves than in the fine roots, except in November when N was remobilized from the leaves. P was similar in fine roots and leaves until November when P was also remobilized from the leaves and P concentrations increased in the fine roots. K concentrations were much higher in fine roots than leaves for most of the season. Ca and Mg concentrations were similar in fine roots and leaves early in season, but were higher in leaves at end of season. Large differences between fine root and leaf micronutrient concentrations were found. Fe and Cu concentrations were about 10-fold higher in roots than leaves, and Zn was about fivefold higher in roots than leaves. Since leaf levels of Zn were at or below the critical

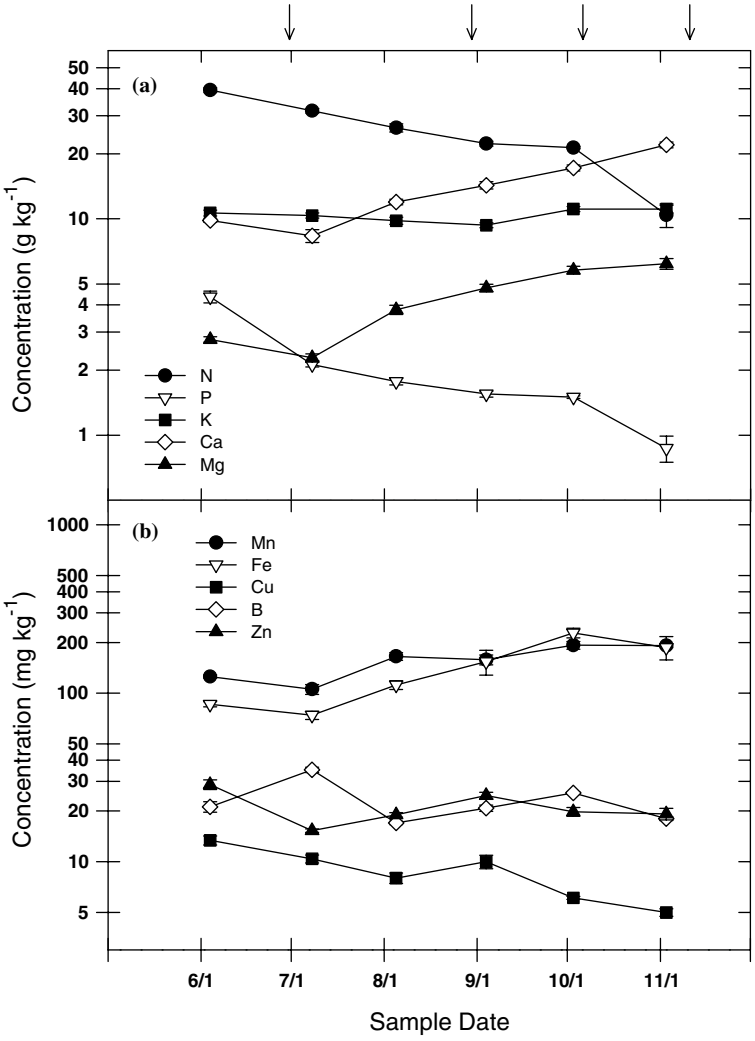

Figure 5. Concentrations of macro- (a) and micro- (b) elements in Pinot Noir leaf blades in 2000. Each symbol represents the mean value with standard error ($n = 8$). Arrows above the figure indicate the time of bloom, veraison, harvest, and leaf-fall. Note the log scale of the *Y*-axis.

concentration for winegrapes (Cook, 1966; Gärtel, 1996; Robinson, 1992), the vines in this study appeared to have difficulty translocating Zn from the fine roots, which had an abundance of this element.

Discussion

The three most important findings from this study were as follows: the majority of grapevine roots (particularly fine roots) and the highest levels of root colonization by AMF occurred within the upper 50 cm of the soil profile in the herbicide-treated vine row; new root growth was most apparent in the fall, beginning about the time of fruit harvest; and finally, the level of arbuscules in fine roots showed consistent seasonal trends, rising sharply in the spring, remaining high throughout the summer and fall, and declining in mid winter.

Fine roots were far more abundant in the topsoil of both the vine row and alleyway than in the subsoil, as compared to woody roots that had a greater relative proportion of their length in the subsoil (Figure 3). The differences observed between the relative distribution of fine and woody roots in the topsoil and subsoil

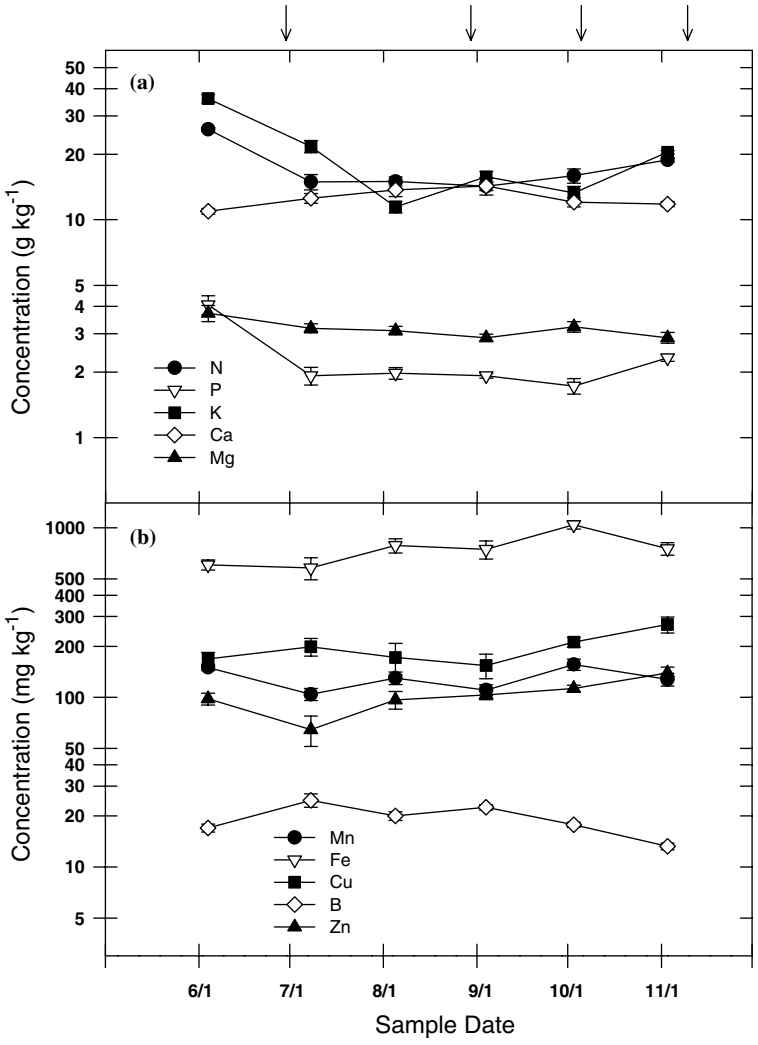

Figure 6. Concentrations of macro- (a) and micro- (b) elements in fine roots of Pinot Noir in 2000. Each symbol represents the mean value with standard error ($n = 4$). Arrows above the figure indicate the time of bloom, veraison, harvest, and leaf-fall. Note the log scale of the *Y*-axis.

suggests that roots have different functions at different depths. Fine roots that proliferated in the nutrient-rich topsoil (Table 2) must have functioned primarily in nutrient uptake, whereas, woody roots that were growing in the subsoil appear to have functioned primarily in water uptake. Numerous researchers have concluded that woody roots of grapevines contribute to water uptake (Mohr, 1996: Richards, 1983; Van Zyl, 1988). Data from this study reinforce that hypothesis because a large proportion (34%) of woody roots with only small fraction of fine roots (10%) occurred in the subsoil where significant water uptake (Figure 2), but surely limited nutrient uptake (Table 2) had occurred. In effect, vines grown under dryland conditions may develop two functionally distinct compartments of the overall root system; a nutrient uptake component primarily located in the topsoil and a water-scavenging component located in the subsoil.

The fine root length data from this vineyard showed that the post-harvest period is the most significant time of new root growth for grapevines grown under Oregon dryland conditions (Figure 3b). These results are not consistent with previous studies that showed maximal root

growth of vines in mid summer prior to harvest (Freeman and Smart, 1976; Mohr, 1996; Van Zyl, 1988). I interpret these findings as follows; the growth of new fine roots generally kept pace with the death of existing fine roots during the spring and early summer, but after harvest (removal of fruit sink) increased carbon flow to the root system and favorable soil moisture conditions produced new roots faster than existing fine roots decayed. This interpretation is supported by findings of fine root lifespan in Concord grapevines grown in the Northeast United States. Roots born in the spring and fall had longer lifespans than roots born in mid summer (Anderson et al., 2003).

The fact that appreciable root growth was not apparent in this vineyard during the early or mid summer period as observed in other grape-growing regions (Freeman and Smart, 1976; Mohr, 1996; Van Zyl, 1988) is most likely related to low soil moisture in this vineyard. Soil moisture was essentially depleted by early August in both years of this study (Figure 2). Grapevines studied by Freeman and Smart (1976) and Van Zyl (1988) were irrigated throughout the growing season, while the vines studied by Mohr (1996) had received five times more rainfall than the vines studied here during the summer months. New root production was probably inhibited by dry soil conditions during mid summer in this study.

The increase in fine root length that occurred in the fall, as rainfall replenished soil moisture, was more substantial in 2000 than in 1999 (Figure 3b). The most logical reason for this was the late fruit harvest that occurred in 1999. Fruit harvest occurred two weeks later in 1999 than in 2000 (Table 1). This resulted in the accumulation of nearly four times more growing degree days during the period from harvest to leaf fall in 2000, as compared to 1999. The longer post-harvest period in 2000 (without the competing fruit sink) would have resulted in greater carbon allocation to the root system and enhanced root growth.

The overall, low density of roots found in this vineyard (Figure 3) agrees with prior studies (Mohr, 1996; Southey and Archer, 1988; Van Zyl, 1988). Grapevine roots must therefore be exceptionally efficient in obtaining nutrients and water. The average density of fine roots over all sampling locations and depths in this vineyard was 0.26 mm mL^{-1} soil, while the average for all roots (woody + fine) was 0.36 mm mL^{-1} soil. Mohr (1996) reported an average value of 0.35 mm mL^{-1} soil of fine roots over the same range of soil depth. These values are an order of magnitude lower than other tree fruit crops (Atkinson, 1980; Bryla et al., 2001). This low root length density appears to result in a high dependency of grapevines on mycorrhizal fungi (Menge et al., 1983; Linderman and Davis, 2001). Indeed, the intensity of root colonization by AMF observed here in grapevines appears to be greater than what has been described in field studies with apple or citrus (Miller et al., 1985; Nemec and Tucker, 1983). The length of extraradical hyphae in this vineyard soil was 19,000 times greater than the length of fine roots. If most of these hyphae were associated with grape roots (as was the case in the vine row where weeds were absent), it is obvious that AMF fungi must greatly facilitate soil exploration by grapevines.

Colonization of fine roots by AMF was greatest where root density was also greatest. AMF colonization was much greater in the topsoil than the subsoil and was greater in vine row as compared to alleyway roots (Figure 4). Colonization of roots in the subsoil was probably limited by the number of AMF propagules in the subsoil, since so few fine roots were growing there. AMF (obligate biotrophs) require the presence of host roots to maintain propagules in soil. However, lower colonization by AMF in grape roots extracted from the alleyway was probably not related to propagule numbers because of the presence of other plants in the alleyway. Roots of the grasses and clover growing in the alleyway were colonized by AMF, averaging 35% of root length colonized in July of 1999. Even though this level of colonization was lower than that found in the grapevine roots (Figure 4), the total quantity of colonized roots supporting AMF in the alleyway soil was much greater than that of the vine row because the root density of alleyway plants was so much greater than that of the grapevines. Reduced colonization of grape roots in the alleyway was most likely due to a disruption of the hyphal network of AMF in soil after cultivating the alleyway soil in the previous year. Tillage effects on AMF are well known and can persist for several years (Johnson and Pfleger, 1992; Sieverding, 1991).

No seasonal pattern was evident in the total colonization of roots by AMF. Hyphae and vesicles present in roots can persist even after roots have begun to decay (Smith and Read, 1997). However, the level of arbuscular colonization in fine roots showed clear seasonal changes that were mostly consistent in both years of the study (Figure 4b). These changes were most evident in fine roots that were growing in topsoil of the vine row. The pattern of arbuscular colonization in these roots indicates that exchange of nutrients between grapevines and AMF occurs from before budbreak until well after leaf fall. A greater level of arbuscular colonization in roots growing in the vine row as compared to roots in the alleyway suggests that roots in the vine row play a more important role in nutrient uptake in this vineyard. This is supported by the fact that higher P and N concentrations were found in the vine row soil as compared to alleyway soil in this vineyard (Table 2). The seasonal patterns observed here for root growth and arbuscular colonization suggests that nutrient uptake and the replenishment of nutrient reserves in grapevines is substantial during the post-harvest period in Oregon, as found in the warmer viticultural regions (Conradie, 1980, 1981a; Peacock et al., 1989). However, the contribution of AMF to nutrient uptake during the post-harvest period may be diminished by high levels of rainfall, as shown by the rapid loss of arbuscules in roots following the unusually wet November of 1999 (Figure 4b).

The concentrations of certain nutrients in fine roots showed larger seasonal changes than expected, suggesting that fine roots may act as important stores for N, P and K. These nutrients were at high concentrations in fine roots at the beginning of the season and decreased substantially by mid summer (Figure 6). While it is well known that the root system as a whole is important in the storage and re-allocation of mineral nutrients (Conradie, 1980, 1981a; Nasser and Kliewer, 1966; Williams and Biscay, 1991), only nitrogen or amino acids have been analyzed over the season in the fine roots of grapevines (Conradie, 1990; Kliewer and Cook, 1971). Seasonal changes that were observed in fine root N concentrations in this study were similar to findings of Conradie (1990) for potted Chenin blanc vines, but were of a greater magnitude. Kliewer and Cook (1971) showed that fine roots contained approximately 50–75% of the arginine concentration found in woody roots. If fine roots contribute substantially to the total root mass, their contribution to storage and re-allocation of N could be significant. The fine root data for P and K found here in Pinot Noir is the first to show that fine roots of grapevines can potentially store and reallocate significant quantities of these nutrients.

Clearly the post-harvest period is a critical time for grapevines to allocate resources to roots under Oregon climatic conditions as indicated by the increase of fine root length found in this study. The high level of arbuscules present in fine roots at this time of year suggests that significant nutrient uptake is likely occurring during the post-harvest period. This idea is not new for grapevines (Conradie, 1980, 1981a), but it has not been supported by whole vine studies from the cooler grape growing regions of North America (Bates et al., 2002; Hanson and Howell, 1995). Even though Oregon is considered a cool climate for viticulture, the warmer air and soil temperatures that occur here in the fall and early winter, as compared to the mid west and northeast United States, probably allows for significant root activity well after harvest. Studies are ongoing to examine whole plant nutrient uptake and allocation patterns in this vineyard. Further work to understand the role of AMF in nutrient uptake of grapevines grown in variety of soils is also being pursued under controlled conditions.

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References

Abbot L K and Robson A D 1984 The effect of root density, inoculum placement and the infectivity of inoculum on the development of vesicular-arbuscular mycorrhizas. New Phytol. 97, 285–299.

Anderson L J, Comas L H, Lakso A N and Eissenstat D M 2003 Multiple risk factors in root survivorship: a 4 year studying Concord grape. New Phytol. 158, 489–501.

Atkinson D 1980 The distribution and effectiveness of the roots of tree crops. Hort. Rev. 2, 424–490.

Bates T R, Dunst R M and Joy P 2002 Seasonal dry matter, starch and nutrient distribution in 'Concord' grapevine roots. HortScience 37, 313–316.

Baylis G T S 1975 The magnoloid mycorrhiza and mycotrophy in root systems derived from it. *In* Endomycorrhizas. Ed. F E Sanders., B Mosse. & P B Tinker. pp. 373–389. Academic Press, New York.

Bethlenfalvay G J, Cantrell I C, Mihara K L and Schreiner R P 1999 Relationships between soil aggregation and mycorrhizae as influenced by soil biota and nitrogen nutrition. Biol. Fertil. Soils 28, 356–363.

Biricolti S, Ferrini F, Rinaldelli E, Tamantini I and Vignozzi N 1997 VAM fungi and soil lime content influence rootstock growth and nutrient content. Am. J. Enol. Vitic. 48, 93–99.

Blee K A and Anderson A J 1998 Regulation of arbuscule formation by carbon in the plant. Plant J. Cell. Mol. Biol. 16, 523–530.

Böhm W 1979 Methods of Studying Root Systems. Springer-Verlag, New York.

Boselli M, Di Vaio C and Pica B 1998 Effect of soil moisture and transpiration on mineral content in leaves and berries of Cabernet Sauvignon grapevine. J. Plant Nutr. 21, 1163–1178.

Bryla D R, Bouma T J, Hartmond U and Eissenstat D M 2001 Influence of temperature and soil drying on respiration of individual roots in citrus: integrating greenhouse observations into a predictive model for the field. Plant Cell Environ. 24, 781–790.

Christensen P 1984 Nutrient level comparisons of leaf petioles and blades in twenty-six grape cultivars over three years. Am J. Enol Vitic. 35, 124–133.

Colugnati G, Boschin A, Bregant F, Tagliavini S and Montanari M 1997 Preliminary results concerning the effects of a new fertilizer for grape nutrition. Acta Hort. 448, 403–410.

Conradie W J 1980 Seasonal uptake of nutrients by Chenin blanc in sand culture: I. nitrogen. S. Afr. J. Enol. Vitic. 1, 59–65.

Conradie W J 1981a Seasonal uptake of nutrients by Chenin blanc in sand culture: II. phosphorus, potassium, calcium and magnesium. S. Afr. J. Enol. Vitic. 2, 7–13.

Conradie W J 1981b Nutrient consumption by Chenin blanc grown in sand culture and seasonal changes in the chemical composition of leaf blades and petioles. S. Afr. J. Enol. Vitic. 2, 15–18.

Conradie W J 1990 Distribution and translocation of nitrogen absorbed during late spring by two-year-old grapevines grown in sand culture. Am. J. Enol. Vitic. 41, 241–250.

Cook J A 1966 Grape nutrition. *In* Nutrition of Fruit Crops. Eds. NF Childers. pp. 777–812. Somerset Press, Somerville.

Freeman B M and Smart R E 1976 A root observation laboratory for studies with grapevines. Am. J. Enol. Vitic. 27, 36–39.

Gardner W H 1986 Water content. *In* Methods of Soil Analysis. Part I. Physical and Mineralogical Methods. Eds. A Klute. pp. 493–544. American Society of Agronomy, Madison.

Gärtel W 1996 Grapes. *In* Nutrient Deficiencies and Toxicities in Crop Plants. Eds. WF Bennett. pp. 177–183. APS Press, St. Paul.

Hanson E J and Howell G S 1995 Nitrogen accumulation and fertilizer use efficiency by grapevines in short-season growing areas. HortScience 30, 504–507.

Hetrick B A D 1991 Mycorrhizas and root architecture. Experentia 47, 355–361.

Hiroyasu T 1961 Nutritional and physiological studies on grapevine. II. Seasonal changes in inorganic nutrient contents. J. Jap. Soc. Hort. Sci. 30, 111–116.

Johnson N C and Pfleger F L 1992 Vesicular-arbuscular mycorrhizae and cultural stresses. *In* Mycorrhizae in Sustainable Agriculture. Eds. G J Bethlenfalvay. & R G Linderman. pp. 71–99. American Society of Agronomy, Madison.

Karagiannidis N, Nikolaou N and Mattheou A 1995 Influence of three VA-mycorrhiza species on the growth and nutrient uptake of three grapevine rootstocks and one table grape cultivar. Vitis 34, 85–89.

Kliewer W M and Cook J A 1971 Arginine and total free amino acids as indicators of the nitrogen status of grapevines. J. Am. Soc. Hort. Sci. 96, 581–587.

Koide R T 1991 Density-dependent response to mycorrhizal infection in *Abutilon theophrasti* Medic. Oecologia 85, 389–395.

Linderman R G and Davis E A 2001 Comparative response of selected grapevine rootstocks and cultivars to inoculation with different mycorrhizal fungi. Am. J. Enol. Vitic. 52, 8–11.

Loubser J T and Meyer A J 1986 Strategies for chemical control of root-knot nematodes (*Meloidogyne spp.*) in established vineyards. S. Afr. J. Enol. Vitic. 7, 84–89.

McGonigle T P, Miller M H, Evans D G, Fairchild G L and Swan J A 1990 A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. New Phtyol. 115, 495–501.

Menge J A, Raski D J, Lider L A, Johnson E L V, Jones N O, Kissler J J and Hemstreet C L 1983 Interactions between mycorrhizal fungi, soil fumigation and growth of grapes in California. Am. J. Enol. Vitic. 34, 117–121.

Miller D D, Domoto P A and Walker C 1985 Mycorrhizal fungi at eighteen apple rootstock plantings in the United States. New Phytol. 100, 379–391.

Mohr H D 1996 Periodicity of root tip growth of vines in the Moselle valley. Vitic. Enol. Sci. 51, 83–90.

Mullins M G, Bouquet A and Williams L E 1992 Biology of The Grapevine. Cambridge University Press, Cambridge. 239 pp.

Nasser A R and Kliewer W M 1966 Free amino acids in various parts of *Vitis vinifera* at different stages of development. Proc. Am. Soc. Hort. Sci. 89, 281–294.

Nemec S and Tucker D 1983 Effects of herbicides on endomycorrhizal fungi in Florida citrus (Citrus spp.) soils. Weed Sci. 31, 427–431.

Newman E I 1966 A method of estimating the total length of root in a sample. J. Appl. Ecol. 3, 139–145.

Nikolaou N, Angelopoulos K and Karagiannidis N 2003 Effects of drought stress on mycorrhizal and non-mycorrhizal Cabernet sauvignon grapevine, grafted onto various rootstocks. Expl. Agric. 39, 241–252.

Peacock W L, Christensen L P and Broadbent F E 1989 Uptake, storage, and utilization of soil-applied nitrogen by Thompson Seedless as affected by time of application. Am J. Enol. Vitic. 40, 16–20.

Petgen M, Schropp A, George E and Römheld V 1998 Einfluss unterschiedlicher inokulationstiefen mit dem arbuskulären mykorrhizapilz *Glomus mosseae* auf die mykorrhizierung bei

reben (*Vitis sp*.) in wurzelbeobachtungskästen. Vitis 37, 99–105.
Possingham J V and Obbink J G 1971 Endotrophic mycorrhiza and the nutrition of grape vines. Vitis 10, 120–130.
Reimers H, Steinberg B and Kiefer W 1994 Ergebnisse von wurzeluntersuchungen an Reben bei offenem und begrüntem boden. Vitic. Enol. Sci. 49, 136–145.
Richards D 1983 The grape root system. Hort. Rev. 5, 127–168.
Robinson J B 1992 Grapevine nutrition. *In* Viticulture. Volume 2. Practices. Eds. BG Coombe. & PR Dry. pp. 178–208. Winetitles, Adelaide.
Schreiner R P 2003 Mycorrhizal colonization of grapevine rootstocks under field conditions. Am. J. Enol. Vitic. 54, 143–149.
Schubert A and Cravero M C 1985 Occurrence and infectivity of vesicular-arbuscular mycorrhizal fungi in north-western Italy vineyards. Vitis 24, 129–138.
Sieverding E 1991 Vesicular-Arbsucular Mycorrhiza Management in Tropical Agrosystems. Deutsche Gesellschaft für Technische Zusammenarbeit, Escborn. 371 pp.
Smith S E and Read D J 1997 Mycorrhizal Symbiosis. Academic Press, San Diego. 605 pp.
Southey J M and Archer E 1988 The effect of rootstock cultivar on grapevine root distribution and density. *In* The Grapevine Root and its Environment. Ed. Van Zyl J L. Rep. S. Afr. Dept. Agricult. Water Supply, Tech. Comm. No. 215, pp. 57–73.
Sylvia D M 1992 Quantification of external hyphae of vesicular-arbuscular mycorrhizal fungi. Meth. Microbiol. 24, 53–65.
Van Zyl J L 1988 Response of grapevine roots to soil water regimes and irrigation systems. *In* The Grapevine Root and its Environment. Ed. Van Zyl J L. Rep. S. Afr. Dept. Agricult. Water Supply, Tech. Comm. No. 215, pp. 30–43.
Williams L E and Biscay P J 1991 Partitioning of dry weight, nitrogen, and potassium in Cabernet sauvignon grapevines from anthesis until harvest. Am. J. Enol. Vitic. 42, 118–122.

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